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James T. McBee
Gulf Coast Research Laboratory

Walter T. Brehm
Gulf Coast Research Laboratory

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SPATIAL AND TEMPORAL PATTERNS IN THE MACROBENTHOS OF ST. LOUIS BAY, MISSISSIPPI

JAMES T. McBEE AND WALTER T. BREHM
Ecology Section, Gulf Coast Research Laboratory
Ocean Springs, Mississippi 39564

ABSTRACT Benthic community structure in St. Louis Bay was studied for 23 months. Cluster analyses distinguished two habitats: open water areas and areas near the marshy shores of rivers and bayous. Two groups of "euryhaline opportunistic" species were dominant at the open water stations. Temporal patterns of the "euryhaline opportunists," which appeared to be controlled by a combination of reproductive pulses and seasonally intense predation, showed that the greatest abundance of macroinfauna occurred during the cooler months with reduced recruitment during the second year. The river-bayou stations were characterized by two groups of "estuarine endemic" species. One of these groups was most abundant in the warmer months and the other in the cooler months. Changes in abundance of the "estuarine endemics" appeared to reflect seasonal cycles.

INTRODUCTION

Early quantitative investigations of benthic macroinfauna were generally concerned with trophic relationships (Petersen 1918). In addition to food web considerations, recent studies have been concerned with the use of benthic macroinvertebrates as biological indicators of water quality and environmental perturbation because of their relative immobility, long life, sedentary habits, and differing tolerance to stress (Copeland and Bechtel 1971, Young 1974). The importance of benthic communities in the ecological description of coastal areas is now well understood, as witnessed by the vast number of environmental impact statements that include benthic studies. If a benthic study is to be more than just a list of fauna collected, it must also describe the distribution and abundance of the species in time and space.

Boesch et al. (1976) pointed out that detailed knowledge of long-term regional community dynamics is necessary to interpret site-specific surveys and that without such knowledge natural variation may be mistaken for the effect of a pollutant, or worse, vice-versa. A few benthic studies have been conducted in the St. Louis Bay, Mississippi, area (Christmas and Langley 1973, Guy 1973, Water and Air Research Inc. 1975, Milligan 1979) but in each case their design, duration or intensity limited their usefulness in providing information about temporal or spatial variation of the benthos. The present effort, a 23-month study of the benthos of St. Louis Bay, was designed to contribute to the knowledge of natural fluctuations of the bottom communities of a low salinity area of Mississippi Sound.

Area description

St. Louis Bay is a mushroom-shaped extension of the western portion of Mississippi Sound (Figure 1). The bay is approximately 10 km wide and 7.3 km long. The mouth is 2.8 km wide. Tides in the area are diurnal with a mean range of approximately 0.5 m. The bay receives fresh water from the Jourdan River on the west and the Wolf River on the east. The northern shores of the bay are fringed by *Juncus-Spartina* marshes. The eastern and western shores are developed as residential property.

Samples were collected at 13 locations in St. Louis Bay (Figure 1) at approximately monthly intervals from December 1977 through October 1979. Stations 1, 3, 5, 9, 11, 17, 18, and 19 were located in open water at depths of 1 to 2 m. Stations 6 and 21 were located about 1 m from the marsh banks of the Jourdan and Wolf Rivers, respectively. Station 22 was also near the marshy shore of Bayou Portage. The substratum at all these stations was sandy mud with considerable organic detritus and the depth was generally less than 2 m. Station 15 was located near the navigation channel in 2.5 to 3.5 m of water. The substratum was very soft grey mud. Station 24 was located on a subtidal sandbar in 1 to 1.5 m of water.

MATERIALS AND METHODS

Benthic infauna was sampled with a 0.023-m^2 Ekman grab. The grab was mounted on a long handle so that depth of penetration (11 to 15 cm) could be controlled, regardless of sediment characteristics, by pushing it into the substratum. At each station, three grabs were collected for infauna and a fourth grab was collected and subsampled for total organic carbon and grain size analyses. *In situ* measurements of surface and bottom water temperature, salinity, and dissolved oxygen were made prior to each collection. Benthic samples were washed into nested sieves with openings of 2.0 and 0.5 mm. Organisms, along with shell fragments, plant debris, and other detritus remaining on the sieves, were preserved in 10% formalin and stained with rose bengal. Organisms were sorted under an illuminated magnifier and stored in 70% ethanol until they could be identified and counted. Faunal data from the three replicates at each collection, hereafter referred to as station-dates, were recorded separately but pooled for analysis. Total organic

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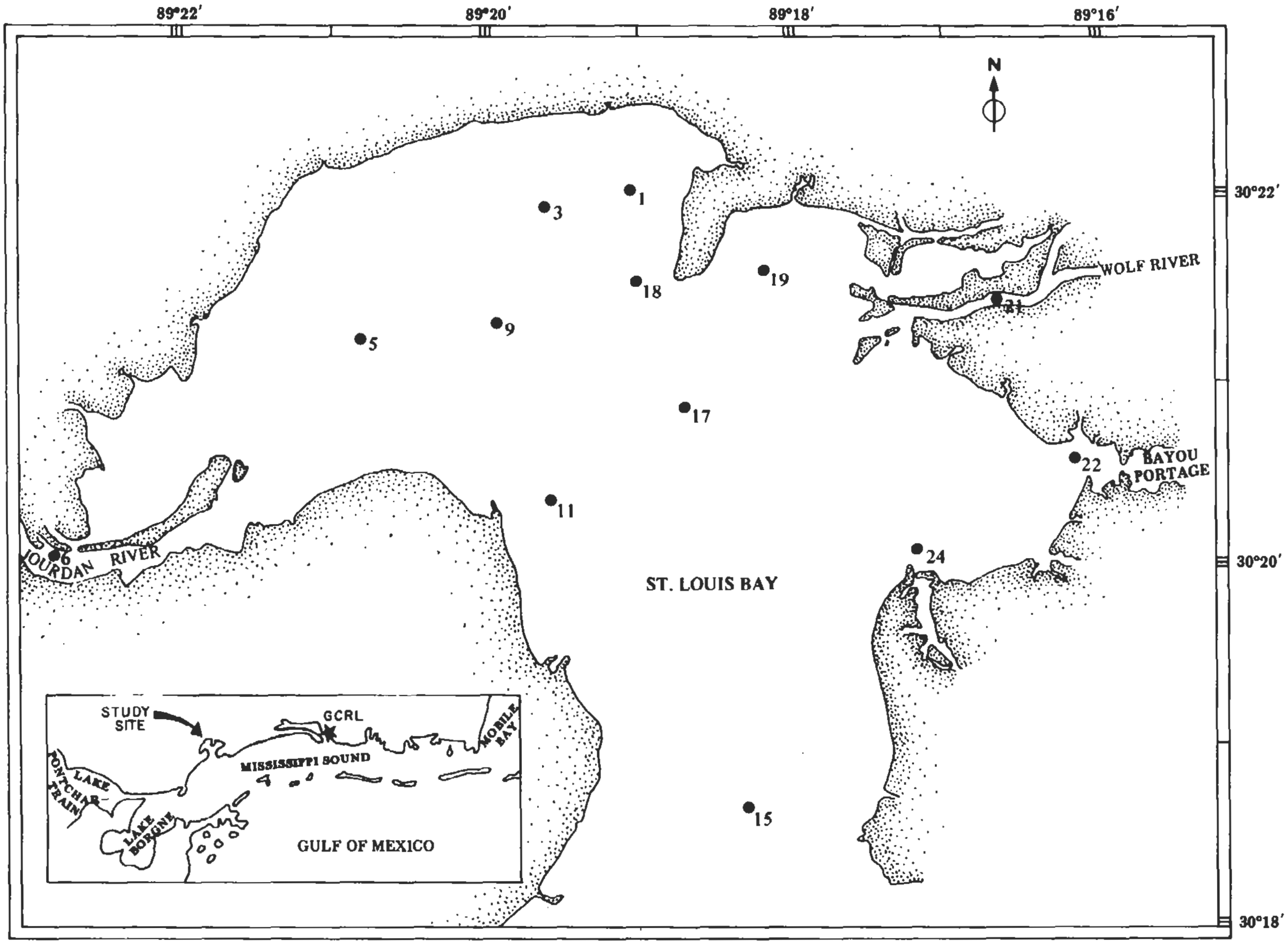


Figure 1. Map of station locations in St. Louis Bay.

carbon and sediment grain size analyses were performed by the Environmental Chemistry and Geology sections, respectively, of the Gulf Coast Research Laboratory (GCRL).

Faunal data were subjected to cluster analysis as a means of showing temporal, spatial, and species associations within St. Louis Bay. The objective of this type of analysis is to group either the entities (station-dates) or the attributes (species) into clusters such that elements within a cluster have a high degree of "natural association" among themselves and are "relatively distinct" from one another (Anderberg 1973). The Bray-Curtis coefficient of dissimilarity was used as the distance measure for these analyses. This coefficient, which is also known as the Czekanowski Quantitative Index (Bloom 1981), can be expressed as either a similarity or dissimilarity index. The dissimilarity form is:

$$D = \frac{\sum_j \left| X_{1j} - X_{2j} \right|}{\sum_j X_{1j} + X_{2j}}$$

where X_{1j} and X_{2j} are the values of the jth variable for the two entities or attributes being compared. In testing four common similarity indices against each other and a theoretical distribution, Bloom (1981) found that only the Bray-Curtis index accurately reflected similarity.

The results of the Bray-Curtis comparisons were sorted using a flexible sorting strategy (Lance and Williams 1966, 1967) with the cluster intensity coefficient, β, set at the conventional value of -0.25. This strategy is intensely clustering and moderately space dilating (Boesch 1977a). Because of a scale problem that exists with all metric coefficients and coefficients derived from metrics (Boesch 1973), a square root transformation was applied so that the largest numbers in the data set were reduced to numbers between 20 and 25 (Dr. William Stephenson, University of Queensland, personal communication). For the inverse analysis, each taxon was standardized by dividing the number of individuals in a collection by the total number of individuals in that taxon. Since very rare species contribute little or no new information to Bray-Curtis analysis, all species taken only three or fewer times during the study were eliminated from the data set prior to analysis. In addition, fish, barnacles, and *Membranipora* sp. were eliminated because of gear selectivity. No reallocation of entities or attributes was deemed necessary.

The cluster analyses were performed using the CLASS program developed by Dr. Robert Smith at the University of Southern California. In order to reduce the size of the data matrix to conform to the program limitations, stations 15 and 24 and the December 1977 samples were eliminated. These eliminations were based on the analysis of the first 13 months of data which showed stations 15 and 24 grouped together for the entire year, and December 1977 collections grouped with those from the first three months of 1978. The grouping of stations 15 and 24 appeared to be the result of their each having reduced numbers of species common to all stations and lacking a unique faunal group. They were, in fact, physically very dissimilar. It was also felt that since December 1977 collections were so tightly grouped with those from the first three months of 1978 they could be eliminated with very little loss of information. These same patterns were shown in the analyses of combined years for stations (summed over time) vs. species and months (summed over stations) vs. species.

Station-date and species groupings were based on the dendrogram and a two-way coincidence table containing the untransformed data. Constancy (in percent) for each species group was determined as the total number of times that the constituent species occurred within a particular station-date group divided by the maximum possible number of occurrences in that station-date group. Fidelity refers to the number of times a species group occurred in a given station-date group divided by the total number of occurrences for that species group.

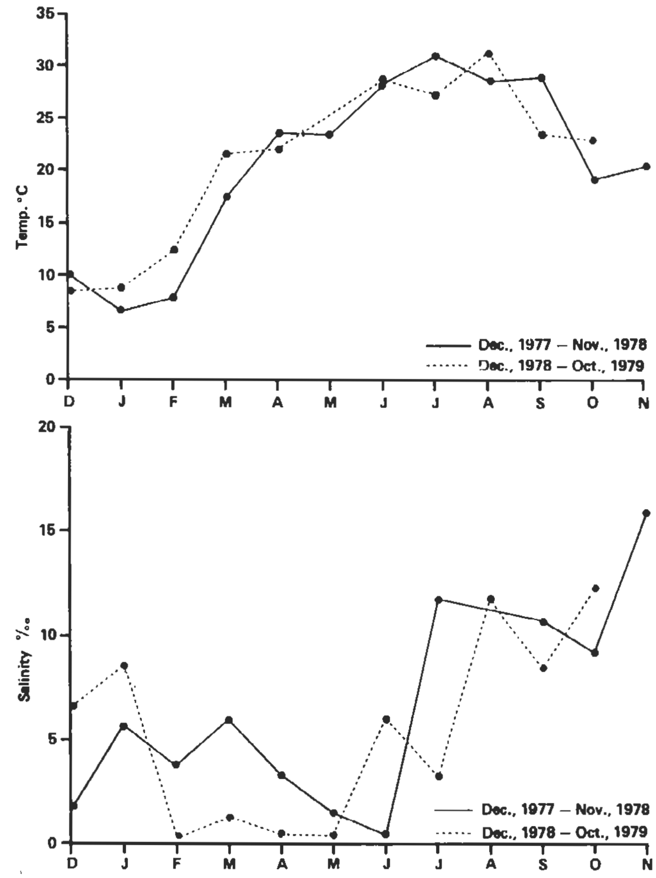


Figure 2. Average bottom water temperature and salinity in St. Louis Bay.

RESULTS

Physical Parameters

Average bottom water temperatures in St. Louis Bay ranged from 6.4 to 31.2°C (Figure 2). The lowest temperatures during both years were encountered during December and January with the highest temperatures occurring in July and August. The general trends among years were very similar with observations never varying more than 4.5°C between the first and second year for any given month. Mean station temperatures for the 23-month period and the results of Duncan's new multiple range test (Table 1a) indicated little difference in temperature among stations.

Average bottom water salinities ranged from 0.3 to 15.8°/$_{\infty}$ over the 23-month period (Figure 2). Although the general trends were somewhat similar, the decrease in winter and spring bottom salinities appeared to be more extreme in 1979 than 1978 and the summer salinities showed a more drastic increase in 1978 than 1979. Average spring salinities appeared to remain lower for a longer period of time during 1979. Duncan's new multiple range test (Table 1b) indicated that the river stations (6 and 21) had significantly lower salinities ($\alpha = 0.05$) than other areas of the bay. The open water stations (1, 3, 5, 9, 11, 17, 18, and 19) showed few significant differences with a high degree of overlap. Stations 15 and 24 had the highest average salinities and were significantly different ($\alpha = 0.05$) from each other and from other areas in the bay.

Differences between surface and bottom temperatures and salinities indicated no long term stratification of the water column. Dissolved oxygen only dropped below 4.5 ppm twice (stations 1 and 5, July 1978) and was not considered critical throughout the study.

Statistical analyses of the measured sediment parameters showed that only the percentage of clay was significantly different ($\alpha = 0.05$) among months. Mean values for each station and significant differences ($\alpha = 0.05$) among stations for each sediment parameter are shown in Table 1c–f. Even though the sediment parameters were correlated to each other, the analyses did not indicate consistent station groupings based upon all four parameters.

Fauna

A total of 79,382 individuals representing ten phyla was collected during 23 months of sampling. We identified 86 distinct taxa including 64 to genus or species level. Polychaetes were the most abundant taxonomic group, accounting for

TABLE 1.

Results of Duncan's new multiple range test showing significant differences ($\alpha = 0.05$) among stations for temperature, salinity, total organic carbon, sand, silt and clay.

a. Temperature °C													
Station	19	24	15	17	3	18	21	5	1	11	22	9	6
Mean Temp.	20.4	20.5	20.5	20.6	20.7	20.7	20.7	20.7	20.8	20.8	21.1	21.2	21.5
b. Salinity ‰													
Station	6	21	5	1	3	19	18	9	11	22	17	24	15
Mean Salinity	3.2	4.0	5.4	5.9	6.0	6.1	6.3	6.4	6.6	6.8	6.8	7.7	9.3
c. Total Organic Carbon %													
Station	24	22	17	18	1	11	19	3	9	5	21	15	6
Mean % TOC	0.6	1.0	1.2	1.3	1.4	1.5	1.6	1.7	1.8	1.8	1.9	2.1	2.6
d. Sand %													
Station	5	15	3	9	1	6	19	18	11	21	22	17	24
Mean % Sand	8.9	11.3	12.2	12.8	15.0	20.5	24.9	25.6	37.1	41.4	52.0	53.1	70.0
e. Silt %													
Station	24	17	11	15	22	21	18	19	3	5	9	6	1
Mean % Silt	15.1	22.5	34.8	35.9	36.3	40.2	40.9	42.5	45.7	49.0	50.1	51.5	53.1
f. Clay %													
Station	22	24	21	17	6	11	1	19	18	9	3	5	15
Mean % Clay	11.7	14.9	18.4	24.4	28.0	28.1	31.9	32.6	33.5	37.1	42.1	42.1	52.8

47.9% of the total number of individuals. Mollusks were the next most abundant group (28.7%) followed by insects (9.3%) and crustaceans (8.1%).

Station groups

Flexible sorting of the station-dates indicated seven major groups (Table 2). Groups I and II are composed of collections from river stations (6 and 21) and the bayou station (22). The major difference between these two groups was the time which these stations grouped together. Group I generally represents the winter-early spring months of both years while group II is composed of collections from summer-fall months for these stations.

Groups III through VII are mainly composed of collections from the open water stations (1, 3, 5, 9, 11, 17, 18, and 19) with each group occurring during a specific time period (Table 2). During 1978 these stations formed three distinct groups: January-May (group III), June-July (group IV) and September-December (group V). Group IV also contained a few samples taken at the river stations (6 and 21) and bayou station (22) during the spring and summer of 1978. Group V also contains a majority of samples taken at the open water stations during June 1979. During 1979 the open water stations were in two time groups: January-March, September and October (group VI) and March, April, July, and August (group VII).

The dendrogram (Table 2) indicates the river stations (6 and 21) and the bayou station (22) (groups I and II) were more similar to each other throughout the study period than they were to the open water stations (1, 3, 5, 9, 11, 17, 18, and 19). Collections taken at the open water stations during the first half of 1978 (groups III and IV) were more similar to each other and to the river and bayou stations than they were to the open water stations during the remainder of 1978 and all of 1979. Collections taken at the open water stations during 1979 (groups VI and VII) were more similar to each other than they were to group V (September-December 1978 and June 1979).

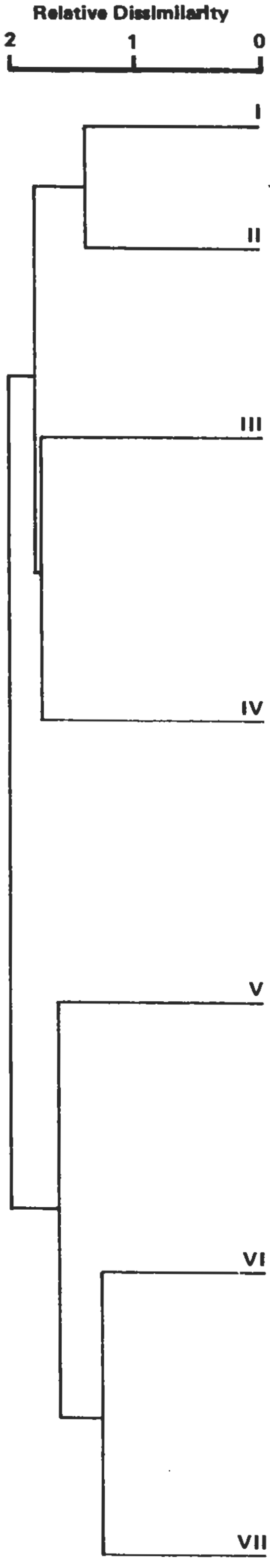
Species groups

Inverse analysis of 22 months of data yielded six species groups (Table 3). The species in group A represent the most abundant benthic organisms in St. Louis Bay (Table 4). Considering each year separately, the highest densities occurred during the winter and spring months at all stations (entity groups I, III, and VI). Recruitment of these organisms appeared to be much higher during the winter of 1978 than 1979. *Hobsonia florida, Streblospio benedicti,* and *Parandalia americana* were the only species in this group that had higher densities at the river and bayou stations during the winter and spring (entity group I) than at the open water stations for the same time period (entity groups III and VI).

The species of group B were most similar to those of group A (Table 3). They were more abundant and had higher constancies in the winter and spring months of each

TABLE 2.

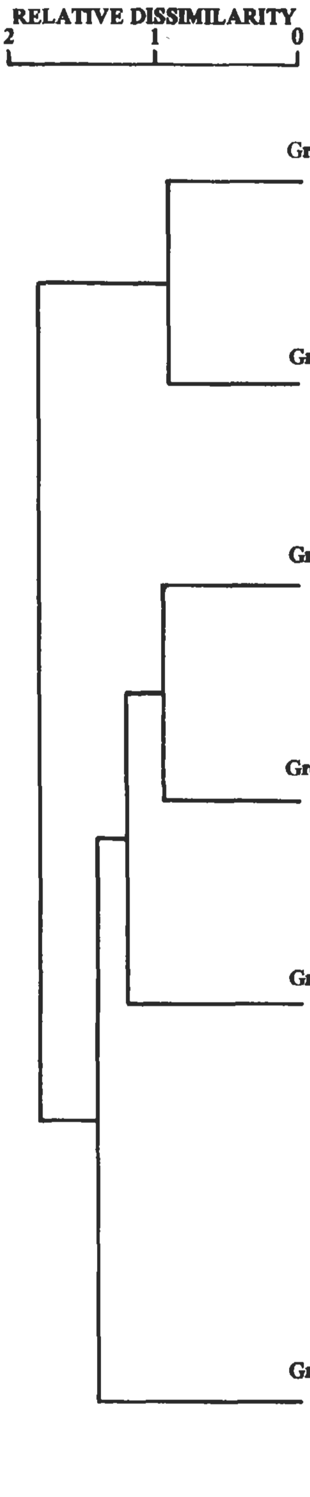
Results of the normal cluster analysis showing the composition and relative dissimilarity of the entity groups. Numbers in the body of the table indicate the station-date composition of each entity group.



Group	1978 J	F	M	A	M	J	J	A	S	O	N	D	1979 J	F	M	A	M	J	J	A	S	O
I	6, 21, 22	6, 21, 22	1, 6, 22	22							6	6	6, 21, 22	6, 21, 22	22	6, 22		22			6	
II					21	21	6, 21	6, 21	6, 21, 22	6, 21, 22	21				6, 21	21	6, 21, 22	6, 21	6, 21	6, 21	21	6, 21
III	1, 3, 5, 9, 11, 17, 18, 19	1, 3, 5, 9, 11, 17, 18, 19	3, 5, 9, 11, 17, 18, 19	1, 3, 5, 9, 11, 17, 18, 19	3, 5, 9, 11, 17, 18, 19																	
IV			21	6, 21	1, 6, 22	1, 3, 5, 6, 9, 11, 17, 18, 19, 22	1, 3, 5, 9, 11, 17, 18, 19, 22	1, 22									17					
V								9, 11, 17	1, 3, 5, 9, 11, 17, 18, 19	9, 11, 17, 18, 19	1, 3, 5, 9, 11, 17, 18, 19	1, 5, 9, 11, 17, 18, 19					11	1, 3, 5, 9, 17, 18				
VI								3, 5, 18, 19		1, 3, 5					11	1, 3, 5, 11, 17, 18	1, 3, 5, 9, 18, 19	11, 19	1, 3, 5, 9, 11, 17, 18, 19, 22	1, 3, 5, 9, 11, 17, 18, 19, 22		
VII											22	3, 21, 22	1, 3, 5, 9, 11, 17, 18, 19	1, 3, 5, 9, 11, 17, 18, 19	1, 3, 5, 9, 17, 18, 19	9, 19					1, 3, 5, 9, 11, 17, 18, 19, 22	1, 3, 5, 9, 11, 17, 18, 19, 22

TABLE 3.

Results of the inverse cluster analysis showing the composition and relative dissimilarity of the species groups.



Group A
Mediomastus californiensis
Micrura leidyi
Macoma mitchelli
Hobsonia florida
Streblospio benedicti
Chironomidae
Parandalia americana
Rangia cuneata

Group B
Ampelisca abdita
Capitella capitata
Haploscoplos robustus
Sigambra bassi

Group C
Cyathura polita
Laeonereis culveri
Grandidierella bonnieroides
Oligochaeta
Rhithropanopeus harrisii
Ceratopogonidae
Cumacea
Hirudinea

Group D
Corophium louisianum
Gammarus tigrinus
Gammarus cf. *mucronatus*
Ostracoda
Hexagenia

Group E
Hargeria rapax
Cerapus benthophilus
Enis minor
Polydora ligni
Eteone heteropoda
Gammarus mucronatus
Geukensia demissa

Group F
Glycinde solitaria
Pectinaria gouldii
Monoculodes edwardsi
Paraprionospio pinnata
Aceton punctostriatus
Amphiporus cruentatus
Edotea montosa
Harpacticoidea
Hydrozoa
Carinoma tremaphoros
Canatellia sp.
Callianassa jamaicense
Diopatra cuprea
Ogyrides alphaerostris
Mysidopsis almyra
Neanthes succinea
Hydrobidae
Callinectes spp.
Nudibranchia
Alpheus heterochaelis

TABLE 4.

Summary table showing the mean constancy and mean number of individuals of each species group within each entity group.

	Entity Group I	Entity Group II	Entity Group III	Entity Group IV	Entity Group V	Entity Group VI	Entity Group VII
Species Group A	95.65*	65.63	98.36	79.91	70.27	82.18	83.75
	66.38†	15.36	59.42	37.92	7.21	21.42	10.12
Species Group B	23.91	2.68	85.53	14.29	21.62	26.06	8.13
	2.04	0.08	7.19	0.50	0.41	0.50	0.11
Species Group C	44.57	59.82	2.96	9.38	2.70	7.18	2.19
	8.83	15.22	0.06	1.55	0.09	0.27	0.04
Species Group D	45.22	16.43	2.11	6.43	0.00	5.53	0.50
	5.12	0.79	0.02	0.27	0.00	0.13	0.01
Species Group E	25.47	7.65	3.38	1.53	0.77	9.12	1.43
	1.85	0.30	0.05	0.02	0.01	0.29	0.01
Species Group F	18.26	11.25	15.13	5.89	13.78	17.13	5.13
	1.56	0.38	1.52	0.23	0.36	0.57	0.07

* Mean constancy in percent.
† Mean number of individuals of each species group within each entity group.

year than during the summer; however, the relative densities of these organisms were much lower than those of species group A for similar time periods (Table 4). The group B species were never very abundant at the river or bayou stations. Like the group A species, recruitment of group B species appeared to be greatly reduced during the winter of 1979.

Species groups C and D were most closely associated to each other and relatively dissimilar to groups A and B (Table 3). The species in these groups were most abundant and had the highest constancies at the river and bayou stations (6, 21, and 22) (Table 4). They had relatively low constancies and mean catches at the open water stations throughout the study period. Differences in these two species groups can be seen in the constancy and mean catch per cell at the river and bayou stations (entity groups I and II). The species in group C were relatively constant and had higher mean catches throughout the study period than the species in group D. Group D species were most abundant at the river and bayou stations during the winter and spring months (entity group I).

Species group E was most closely associated with the river and bayou stations, however, they were taken relatively infrequently. Species group F was loosely formed. These taxa were generally collected sporadically in relatively low numbers throughout the sampling period.

DISCUSSION

Spatial variation

Several investigators have demonstrated changes in benthic faunal assemblages based on gross changes from sand to mud sediments (Sanders 1958; Tenore 1972; Polgar 1975; Mountford et al. 1977; Whitlach 1977; Loi and Wilson

1979; Maurer et al. 1979). However, Boesch (1973) found that most macrobenthic species in Hampton Roads, Virginia, were either not bottom-type specific or were restricted in varying degrees to sand bottoms. Except for station 24, all of the sample sites in this study averaged less than 54% sand, indicating mud or sandy mud sediments. The station-date dendrogram (Table 2) and the Duncan's multiple range test for sand (Table 1d) show no consistent pattern between the groupings of stations based on percent sand and the distribution of benthic infauna in St. Louis Bay.

Sanders (1958) also found that the distribution of dominant deposit feeders, the predominant trophic type represented in this study, correlated with percent clay composition of the mud sediments. Other investigators (McNulty et al. 1962, Santos and Simon 1974, Maurer et al. 1978) have shown the clay fraction to be relatively unimportant in influencing the distribution of deposit feeders. Station groupings in the station-date dendrogram (Table 2), determined mainly by the distribution of deposit feeders, show no relationship to those groups based on percentage of clay in the sediment (Table 1f).

Most estuarine organisms have a wide range of habitat selection. Sedimentary effects in estuaries are confounded with other environmental parameters such as depth, salinity, and seasonal changes (Tenore 1972). Boesch (1973), Watling (1975), and Whitlach (1977) reported benthic faunal assemblages from the east coast which were ubiquitous within their respective study areas. In addition, Boesch (1973) also denoted a seasonally restricted species group. Two species groups in this study showed a similar distribution. Species group A contained the numerically dominant organisms and were taken consistently at all stations (> 65%, Table 4). Species group B appeared to be seasonally restricted. They had the highest constancies during the winter and spring months (entity groups I, III, V, and VI).

Salinity is known to play an important role in the distribution of estuarine faunal assemblages. Tenore (1972) and Maurer et al. (1978) denoted a transition in benthic assemblages associated with a change from oligohaline ($< 5‰$) to mesohaline ($5-18‰$) waters in bays along the east coast. Boesch (1977b) stated that "euryhaline opportunistic" species decline in importance and number upestuary as their salinity tolerance limits are reached (approximately $5‰$). "Estuarine endemic" species become more abundant below $5‰$.

The benthic faunal assemblages in St. Louis Bay exhibited a similar pattern. Species groups A and B were dominant throughout the sampling area. Salinities in open water portions of the bay conform to the range given by Boesch (1977b) for "euryhaline opportunists" and many of the species in these groups have been termed opportunistic by other investigators. Analysis of variance showed the river stations had significantly ($\alpha = 0.05$) lower salinities than the rest of the sampling area (Table 1b) with means $< 5‰$. The species in groups C and D were faithful to these stations (87% and 76% fidelity, respectively). These species appear to be "estuarine endemic" and are important only in areas immediately adjacent to freshwater inflow. The bayou station (22) appeared to be transitional between the river and open water stations. It was located near an intermittent source of fresh water and the "estuarine endemic" species (groups C and D) were generally present when station 22 grouped with the river stations. The species in these two groups were uncommon during the periods when station 22 grouped with the open water stations.

Temporal changes

Various patterns of temporal variability in the benthos have been reported. In Delaware Bay, Watling (1975) reported repeating seasonal cycles with greatest infaunal density in June and the lowest in October. Lie and Evans (1973) found strong seasonal changes in Puget Sound, Washington; however, when compensated for seasonal variability they reported great year-to-year stability. Poore and Rainer (1979) found no seasonality in Port Phillip Bay, Australia, but rather strong aperiodic changes in the density of the common species and in the composition of the subdominant fauna. Along the temperate east coast of the United States, Tenore (1972), Boesch (1973), Holland et al. (1977), and Whitlach (1977) have all reported seasonal changes in benthic infauna with greatest densities in the winter and spring. Benthic studies along the northern Gulf of Mexico coast by McBee and Brehm (1979), Johnson (1980), and Sikora et al. (1981) showed seasonal changes with the greatest density in the cooler months. Sikora et al. (1981) found repeating seasonal cycles; however, Johnson (1980) noted a continuous change in community structure throughout his study.

The nature of temporal changes of the benthic infauna in St. Louis Bay varied with habitat type. Seasonal changes at the river and bayou stations appeared to be cyclic. These stations clustered mainly in two groups: the cooler months of both years (group I), and the warmer months of both years (group II). Among the "estuarine endemic" species, group C was dominant throughout the study period. These species generally had seasonally comparable densities throughout both years with abundance peaks in the warmer months. Species groups D and E also had seasonally comparable densities during both years; however, they were only abundant during the cooler months.

The temporal variation at the open water stations was a result of fluctuations in abundance of the species in groups A and B. Species of these two groups, which had their highest constancy and abundance from January through May 1978 (group III), showed marked reductions in density during the warmer months (group IV). These reduced numbers continued through December 1978 (group V). The second year did not group, season-by-season, with the first year because of greatly reduced numbers of group A species and the paucity of group B species. During 1979 the September and October samples from the open water stations grouped with the winter and spring months (group VI). This was apparently the result of an early fall recruitment with numbers approximating those of the delayed recruitment from the winter. The warmer months of 1979 generally formed a group (VII) which separated from 1978 because of greatly reduced numbers in the second year. This indicates that the open water stations may show cyclic changes in some years and aperiodic changes in others. Lack of uniformity such as this underscores the need for long term studies in any attempt to understand the dynamics of estuarine benthos.

Temporal changes in the benthos have been attributed to various causes. Seasonal spawning pulses were suggested by Tenore (1972), Boesch (1973), Holland et al. (1977), and Whitlach (1977). Predation of adult or larval forms was thought to be important by Thorson (1966), Boesch (1973), Boesch et al. (1976), Virnstein (1977), and Cammen (1979). The depletion of benthic infauna in the summer months was linked to low dissolved oxygen concentrations by Tenore (1972), Holland et al. (1977), and Johnson (1980). Johnson also found changes in community structure related to drastic changes in salinity caused by a near-record flood following a prolonged drought. High mortality rates of newly set larvae caused by indiscriminant settling was mentioned by Cammen (1979) and Sikora et al. (1981).

There is undoubtedly a variety of mechanisms responsible for the temporal patterns observed in the St. Louis Bay infauna. The recruitment seen in the cooler months of both years was almost certainly caused by newly set juveniles because of the small size of the individuals. This is consistent with the seasonal spawning pulses observed along the temperate east coast of the United States.

Foraging by fishes is undoubtedly important to the fluctuations of the benthos of St. Louis Bay, particularly for the more abundant species (groups A and B). Darnell (1958) and Overstreet and Heard (1978) reported over 65% of the species in groups A and B from the stomachs of spot (*Leiostomus xanthurus*) and Atlantic croaker (*Micropogonias undulatus*). Cage studies have also indicated the importance of predation on benthic macroinvertebrates. Naqvi (1968) reported that the number of animals inside cages in Alligator Harbor, Florida, was four times the number in the surrounding substratum. Virnstein (1977) found that species populations in Chesapeake Bay were not resource limited but rather predator controlled. Trawl collections by the Fisheries Research and Development Section of GCRL (Dr. Thomas McIlwain, personal communication) showed that juvenile spot and croaker moved into St. Louis Bay in great numbers from May through July 1978 and April through July 1979. These months correspond to the times of reduced abundance of the species in groups A and B.

Dauer (1974) showed that in Tampa Bay, Florida, the majority of benthic macroinvertebrates spawn more or less continuously. If summer spawning occurs in St. Louis Bay, predation on planktonic larvae may be an important factor. Boesch et al. (1976) discussed the impact of predation by the ctenophore *Mnemiopsis leidyi* on planktonic larvae of benthic macroinvertebrates. Unpublished data (Dr. Robert Woodmansee, GCRL, personal communication) show that *M. leidyi* was absent from the plankton during periods of greatest recruitment of group A benthic species and abundant during the months when recruitment was slight. The presence of this voracious planktivore could be important in limiting the success of recruitment during the warmer months. Thus, except possibly for extreme years, St. Louis Bay appears to exhibit physically controlled spatial patterns and biologically controlled temporal variability among the benthic macroinvertebrates.

Faunal comparisons

Comparison of the species taken in this study with those of similar studies along the Atlantic coast indicated that, except for lower Chesapeake Bay, few species were common to both areas. Boesch (1977b) reported 75 species from the York River area but only 16 of those were found in St. Louis Bay. In the Hampton Roads area, Boesch (1973) collected 168 species including 21 which were taken in this study. However, if only those species that were determined to be abundant enough to be used in the cluster analyses of each study were compared, the number of co-occurring species dropped to 13. Species groups defined by Boesch using cluster analysis for the York River and Hampton Roads areas were unlike the species groups of this study. Of the 74 species reported by Mountford et al. (1977) from the Calvert Cliffs area, 20 were found in St. Louis Bay. Comparing only the species that were considered abundant, only 8 were common to both areas. Based on these studies, 10 species (*Aceton punctostriatus, Cyathura polita, Eteone heteropoda, Glycinde solitaria, Monoculodes edwardsi, Neanthes succinea, Paraprionospio pinnata, Pectinaria gouldii, Polydora ligni,* and *Streblospio benedicti*) were abundant in the three areas of the lower Chesapeake Bay and St. Louis Bay. Other studies from the east coast (Tenore 1972, Polgar 1975, Watling 1975, Whitlach 1977, and Cammen 1979) contained fewer than 8 species that were found in St. Louis Bay.

Benthic community studies in Gulf of Mexico estuaries indicated varying degrees of species similarity. Santos and Simon (1974) reported 44 species of polychaetes from Tampa Bay. Nine of those were also found in St. Louis Bay, and 3 (*Capitella capitata, Laeonereis culveri,* and *Streblospio benedicti*) were among the more abundant organisms in both studies. Johnson (1980) listed 25 species from Mobile Bay, Alabama, which were also collected in St. Louis Bay. However, of the 21 most abundant species listed by Johnson, only 5 were found in St. Louis Bay. *Mediomastus* *californiensis* was the most abundant benthic macroinvertebrate in both studies but the remaining 4 species (*Diopatra cuprea, Glycinde solitaria, Neanthes succinea,* and *Paraprionospio pinnata*) were taken relatively infrequently in St. Louis Bay. Species groups reported by Johnson were unlike the groups seen in this study. Sikora et al. (1981) reported 30 taxa from Lake Pontchartrain, Louisiana; however, 2 species of hydrobid gastropods (*Probythinella louisianae* and *Texadina sphinctostoma*) made up 86% of all individuals. Most of those taxa were found in St. Louis Bay but the hydrobids were seen only occasionally. The infauna of Trinity Bay, Texas, (McBee 1975) showed the highest degree of similarity to the benthic community of St. Louis Bay. Thirty species were reported from grab samples in Trinity Bay and 19 of these were also collected in St. Louis Bay. *Mediomastus californiensis* was most abundant in Trinity Bay as it was in St. Louis and Mobile Bays. Cluster analysis in the Trinity Bay study produced a ubiquitous and abundant species group which was nearly identical to group A of this study. No other group similarities were noted.

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